Invasive Species Increase Biodiversity and, Therefore, Services: An Argument of Equivocations

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Abstract

Some critics of invasion biology have argued the invasion of ecosystems by non-indigenous species can create more valuable ecosystems. They consider invaded communities as more valuable because they potentially produce more ecosystem services. To establish that the introduction of non-indigenous species creates more valuable ecosystems they defend that value is provisioned by ecosystem services. These services are derived from ecosystem productivity, the production and cycling of resources. Ecosystem productivity is a result of biodiversity, which is understood as local species richness. Invasive species increase local species richness and, therefore, increase the conservation value of local ecosystems. These views are disseminating to the public via a series of popular science books. Conservationists must respond to these views, and I outline a method of rejecting such arguments against controlling invasive species. Ecological systems are valuable for more than local productivity and biodiversity is not accurately described by a local species count.

Keywords: Invasive Species; Beta-Diversity; Biodiversity Concept; Ecosystem Services; Option Value; Invasive Species Scepticism

Introduction

It is common practice throughout the world to control invasive species populations to maintain the character and composition of ecological communities. Invasive populations are controlled through the reduction or elimination of their populations and preventing their movement into new areas (Kopf et al. 2017). Scepticism towards the control of invasive species populations has flourished recently with a series of scientists, environmental journalists, and other academics arguing there is rarely reason to control invasive species (Sagoff 2005; Marris 2011; Thompson 2014; Pearce 2015; Thomas 2017). This movement has been described as invasive species denialism, and while there are moments when this literature tips into denialism, there are legitimate arguments that warrant serious consideration (Russell & Blackburn 2017; Frank 2019). In this paper, I draw out and critique an argument that has coalesced within the Invasive Species Sceptics (who I will refer to as *sceptics*) literature. This argument is separate from the standard animal welfare-based arguments that motivate the "compassionate conservation" movement (Wallach et al. 2018) or arguments that concepts such as 'nativeness' or 'invasive species' are not well-defined or useful (Chew & Hamilton 2011). Instead, the argument addressed here proposes that invasive species are, all things considered, not bad for humanity. I aim to clearly represent the argument, so that scientists may directly address it, and illustrate some possible responses. In my view, the argument pivots on what I consider an illegitimate use of the concept 'biodiversity'. The sceptics equivocate between their interpretation of 'biodiversity', and indeed 'ecosystem services' as well, and the interpretations of these concepts which are more common to conservation science to make it appear that their position is not as radical as it is. Their argument against the control of invasive species can be found scattered through multiple sources and can be reconstructed as follows:

Why we should not control invasive non-indigenous species:

1. We should not control populations if they promote ecosystem services (more than any readily available alternative).

2. Invasion often increases *biodiversity*.

3. More *biodiversity* results in more *ecosystem services*.

4. Invasive species often promote *ecosystem services*. (2, 3)

Conclusion: We should not control invasive species as they often promote ecosystem services (1, 4)

This is an extrapolation of a more moderate position, which states that invasive species can contribute to ecosystem services and we should not control a population when these contributions are on sum worth more than the cost of population control (Davis et al. 2011). The above argument generalises the particular, stating on sum we are not warranted acting on invasive species. This implies that research is required to justify preventing the movement of a population into wilderness areas or eradicating a population while it has a small abundance and before it substantially impacts an area. Both positions somewhat utilise the difficulty in conducting cost-benefit analyses of species impacts to support inaction (Courtois et al. 2018). While some may claim this strong view is a fringe argument of a small vocal minority, this is only true internally to the field of conservation science itself. Several of the books that defend this view received wide media attention, particularly *The New Wild* (Pearce 2015). These views are disseminating through the public and it is critical to stakeholder engagement for conservationists to respond to these arguments.

The idea that invasive species increase biodiversity, and in turn ecosystem services, is unsurprising given the dominant paradigms in conservation ecology, found within the Biodiversity-Ecosystem Services (BES) literature. It has only really been reapplied, with some modifications, to new conclusions by the sceptics (Sagoff 2005; 2018; Pearce 2015; Thomas 2013; 2017) or accepted as an implication of the BES framework (Odenbaugh 2020). This argument can also be converted into a reductio against the BES conservation framework (Newman et al. 2017). In Section 2, I flesh out the argument and situate it in the literature. I critique the argument for deploying impoverished operationalisations of key conservation concepts, biodiversity and ecosystem services. In Section 3, I discuss how ecosystem productivity fails to encompass the range of services proposed within the Ecosystem Services conservation framework. In Section 4, I turn to how local species richness misses many of the critical values the 'biodiversity' concept was designed to encompass. Finally, I conclude by conceding some roles Non-Indigenous Species play in contributing to biodiversity (Section 5).

2. Unpacking the argument

2.1. Environment as a service provider

The initial premise, *"(w)e should not control populations if they promote ecosystem services",* is a corollary of the position that we should preserve species because they provide ecosystem services. Following the Millennium Ecosystem Assessment (MA), which found that ecosystem degradation was a major threat to current and future human wellbeing, ecosystem services have become a major focus of conservation (MA 2005). Ecosystem services are, "the conditions and processes through which natural ecosystems, and the species that make them up, sustain and fulfill human life" (Daily 1997, p. 3). More generally, they are considered goods of immediate economic utility. Varying interpretations of "ecosystem services" has led to a literature in which the empirical work, ethical work, and conceptual work do not always lead to the same conclusions about what is worthy of conservation.

There is serious debate about what of nature's value is captured by ecosystem services (Schröter et al. 2014). Under some interpretations, anything related to our immediate preferences for nature can be labelled ecosystem services. Conservationists often raise values they believe are not contained within the ecosystem services framework, only to find those within the framework replying that the value raised against them are included (e.g., option value in Faith 2010; Perrings et al. 2010). Sometimes it appears that ecosystem services proponents state a type of value can conceptually be part of the services framework without indicating how the biological features their experiments quantify represent this source of value. A crucial example of this is that many experiments examining the relationship between biodiversity and ecosystem services use biomass production, or net primary production, as a proxy for ecosystem services generally (Newman et al. 2017).

Biomass produced is not representative of the range of values people have towards the environment, but it is readily measurable and represents ecosystem productivity. There is a neat conceptual connection between biodiversity, functional diversity, and ecosystem productivity. The thought being biodiverse assemblages will be functionally diverse, providing many ways to process resources, with diverse processing and specialisation the ecosystem will be highly productive. This is appealing as each component is readily quantifiable. Strong proponents of the premise that ecosystem services are the sole justification for conservation can be found within the BES literature as much as within the invasive species sceptic literature, some of whom recognise other types of environmental values (see Marris 2011). For example, Dasgupta et al. (2013) represent biodiversity as only being valuable insofar as it provides ecological functions that can then make productive ecosystems.

The representation of biodiversity as only being justified through its relationship to the production or cycling of resources diminishes the variety of values associated with biodiversity. Sometimes biodiversity is represented as either being valuable as it is a cause of services or it has *intrinsic value,* which is notoriously difficult to quantify and whose existence is contested (e.g. Reyer et al. 2012). This all creates the perception, whether justified or not, that biodiversity only derives value from its provision of a narrow set of services, usually equated with resource production and cycling. This underemphasises the cultural, regulating, and supporting services ecosystems provide. It is this narrow interpretation of the relationship between biodiversity and ecosystem services, or more commonly the accidental use of language which represents this relationship as narrow, which warrants the conclusion we should not control invasive species.

2.2. Invasive Species increase Biodiversity

Despite many invasive species causing local extinctions, their addition to new ecosystems does not necessarily lead to drastic species loss. There is strong evidence that local species richness worldwide has recently either remained stable or increased (Sax & Gaines 2003; Dornelas et al. 2014). Invasive species can increase the number of species locally; as Pearce (2015 p. 9) says “Rather than reducing biodiversity, the novel new worlds that result [from invasives] are usually richer in species than what went before". Local species numbers generally appear to be a product of the regional pool of species (Ricklefs 1987). With global connectivity increasing (the *'New Pangea'* celebrated by Thomas 2017), so has the 'regional' species pool. This has ultimately driven up local species richness.

Assessing species richness is not a simple process. Sometimes ecologists exclude non-indigenous species from local species counts, but as Sagoff (2005 p. 229) argues excluding these populations from such counts by stipulation is just dodgy accounting. But contra Sagoff and other critics of invasive species science and management, any semantic argument utilizing species richness without effort to address the complexities of scale will misrepresent the natural patterns of species distributions. Representing species diversity at multiple scales cannot be done with any single equation (Whittaker et al. 2001).

Local increase in species richness has been coupled with global species loss (Dirzo & Raven 2003). This phenomenon has been described as 'the biodiversity paradox' (Vellend 2017). The explanation for the paradox is evident, if you add many common non-indigenous species to an area but lose fewer endemic or rare native species there will be increasing local species counts and global species loss. Australia (and the world) has lost the desert bandicoot (*Perameles eremiana*) but gained the red fox, cat, black rat, and common pigeon; a triumph!

Ultimately, this indicates simply discussing species numbers misses much of the picture in ecological systems. There must be some attempt to address the relationships between populations. Co-evolved populations have interdependencies, which invasive species can disrupt causing cascading extinctions (Simberloff 2013). While such losses can be recouped through introducing more species, the losses are significant for community composition. The species lost are often specialists who are co-adapted to other local species, the populations introduced are often generalists who can utilize a range of resources and live within varied conditions (Clavel et al. 2011). This leads to the global loss of functional diversity as generalist species prosper. The structure of species interactions must be incorporated into any picture of conservation due to how these interdependencies both lead to species loss and structure biodiversity.

2.3. Biodiversity Yields Ecosystem Services

The next step in the case against invasive species control is that the increase in local species counts, due to the introduction of non-indigenous species, results in more ecosystem services. The BES research program supports the case for invasive species increasing the value of ecosystems. There is a great deal of evidence, predominantly from plants assemblages, that biodiversity increases ecosystem functioning, which increases ecosystem services (Loreau et al. 2001, Haines-Young & Potschin 2010, Mace et al. 2012). If non-indigenous species increase biodiversity, then they increase the ecosystems services, which facilitate nature's value to humanity. Or as Mark Sagoff states, "If in any scientific (e.g., random) sample of ecosystems introduced organisms generally, overwhelmingly, and typically increase species richness, and if species richness supports desirable ecosystem properties, then one could argue these organisms benefit those systems." (Sagoff 2005 p. 225).

The BES research program has predominantly considered the effects of biodiversity as measured in species richness on ecosystems (Hendriks & Duarte 2008). The most studied effect variable of the biodiversity and ecosystem services relationship is the extent to which ecosystems produce biomass (Cardinale et al. 2011). The scales assessed in these experiments are generally local, only occurring over scales up to 100m. Conservation policy likewise is conducted on the scale of hectares (Srivastava & Vellend 2005). Srivastava and Vellend (2005) take this as evidence that we should be sceptical of the significance of the biodiversity-ecosystem services relationship in conservation, while the sceptics' take this local scale relationship as support of their view. The scales considered by the science, and the policy, can be understood as supporting the sceptics' conclusions that we should not control populations of invasive species as on local scales they generally increase species richness and, therefore, ecosystem services.

3. Ecosystem Services: Problems with Productivity

Even granting the primacy of ecosystem services in conservation policy, these services come with deceptive variations in how tangible and quantifiable they are. The Millennium Ecosystem Assessment identifies four types of service: provisioning (e.g., wood), regulating (e.g., water quality), cultural (e.g., recreation), and supporting (e.g., carbon cycle) (MA 2005). Despite the scope of the services described, the empirical research on such services historically has narrowed its focus to predominantly the relationship between species richness and biomass or net primary production (e.g., Carpenter et al. 2006; Costanza et al. 2007; Cardinale et al. 2011). Ecosystem productivity undoubtedly influences the different forms of services provided, it is crucial for both the provision of resources and the regulation of resource cycles. But the emphasis on resource production and cycling to the exclusion of other modes by which services are provided, particularly cultural services, stack the deck towards invasive species. One could counter that ecosystem services are more widely measured than biomass, which is true (Costanza 2015). The issue, however, is that services have historically disproportionately used biomass as a proxy (Newman et al. 2017), which allows for this style of argument to be constructed. Echoes of this historical trend can be seen in the modern literature, a recent metanalysis shows that while ecosystem production and ecosystem provisioning of services was measured by 67% and 68% of studies, only 35% measured the cultural services ecosystems provided (Boerema et al. 2017).

Invasive species can contribute to services and reduce services, often simultaneously doing both, and empirical research is required to determine to what degree (Boltovskoy et al. 2018). But the relative contribution of species to the productivity of an ecosystem is highly influenced by the sheer abundance of that population (Winfree et al. 2015). This makes ecosystem productivity quite antithetical to conservation's aims of preserving endemic and rare species, which are often not abundant. Many rare, threatened, and endangered species are 'functionally extinct' in that they are not able to have strong effects on the ecosystem they reside within. Within a BES framework, where productivity and direct causal contribution is emphasised, such species lack value. Instead, it is the hyper-abundant and highly productive species that contribute. The features that make invasive species invasive rather than just non-indigenous is their ability to rapidly grow in abundance and exclude other populations through their consumption (Simberloff 2013). Their ability to produce biomass, or 'cycle' biomass to through predation or herbivory to disproportionally increase their representation, is what allows them to physically exclude local species. These properties are given a new presentation by sceptics, their rapid increases in abundance and biomass make them productive ecosystem services providers (Pearce 2015). Invasive species then should be considered as 'super species' due to their success moving across the globe and processing biomass (Hamilton 2010). It is the framing of biodiversity's value as being strongly connected to the productivity of whole ecosystems that leads to these conclusions.

Conservationists have warned against strongly connecting conservation to ecological productivity (Silvertown 2015; Faith 2018). Following his reflections on Leopold's land ethic Michael Soulé warned us that justifying conservation through ecosystem processes would facilitate the conclusion we should replace native species with invasives:

> *"it is technically possible to maintain ecological processes, including a high level of economically beneficial productivity, by replacing the hundreds of native plants, invertebrates and vertebrates with about 15 or 20 introduced, weedy species…. WARNING! Be suspicious of "ecologists" who are pitching ecological services (for people) and who speak of "redundant" species or "hyperdiversity.""*
>
> Soulé 1996 (p. 60)

In the face of such warnings we now find, two decades on, significant support for the idea invasive species are 'super species', which can replace natives due to their productivity (e.g. Pearce 2015).

4. Biodiversity

4.1. Biodiversity is more than Species Richness

In the case of invasive species being added to the local species pool, biodiversity is increased under the assumption that biodiversity is local species richness (Pearce 2015; Thomas 2017). Invasive species sceptics expect this increase to outpace local species extinctions. Local species count, or species richness, is widely known as α (Alpha) diversity. When the local extinctions are of species endemic to that region, global species counts reduce. This global inventory of species is γ (Gamma) diversity, or more accurately the inventory of all the local systems being analysed. These two diversity measures take an inventory of the populations or species or similar unit of biodiversity in their region. There is another count, which is widely considered an essential target in conservation. This is β (Beta) diversity, which is a comparative measure of diversity between regions. It considers how many new species are added to the regional species pool by an area. By taking biodiversity as only α diversity, sceptics significantly underplay the damage Non-Indigenous Species do by diminishing γ diversity and β diversity.

β diversity is a measure of the entities which comprise biodiversity, biodiversity units; these are generally counted as species but can be other entities (Sarkar 2016). For example, the entities being counted could be the distinct habitat types in an area, like shrublands or deciduous tree forest, or biotic 'features', which are the biotic traits possessed by populations such as their genes or their 'functions'. Further dimensions of biodiversity could be argued for such as diversity of biotic interactions (Luna et al. 2020). These can be understood as compromising different levels of biodiversity and we may have reason to count all or some (Faith 2016; Lean & Sterelny 2016). A local ecosystem will have higher β diversity the more unique biodiversity units it adds to the previously assessed regional pools, the 'complementary' units of diversity (See Figure 1). If there are no previously assessed areas, then we are making a count of biodiversity units in an area, which is equivalent to α diversity.

Insert Figure 1.

Adding new species to those already protected increase β diversity but species are not equivalent. Many species are extremely similar (e.g., cryptic species). Complementarity has been incorporated into algorithms to identify species that are the least similar to each other (Vane-Wright et al. 1991; Faith 1992). The disparity between species can be represented through measuring their phylogenetic distance or the functional differentiation (see Magurran & McGill 2011). There are continuing debates on which measures best represent biological difference but incorporating the extent to which populations themselves contribute unique features is an extension of complementarity and biodiversity measurement (Lean & Maclaurin 2016; Lean 2017).

β diversity is generally thought of as an essential component of biodiversity preservation practice (Sarkar 2012; 2016; Socolar et al. 2016). This is partially due to a conceptual claim, biodiversity as a concept is designed to maximize the representation of difference or variety in life forms. Regardless of the entities measured as representing biodiversity, higher β diversity results in more biotic variety, therefore, should be incorporated into conservation decision-making (Sarkar 2006). Complementarity already has featured in the practice of conservation planning for 40 years to select areas that represent the most distinct lifeforms (Kirkpatrick et al. 1980). It is both part of the practice of conservation and part of the theoretical framework of biodiversity conservation. Insofar as biodiversity aims to represent more than just a tally it must quantify unique entities.

4. 2. Valuing Biodiversity beyond Species Richness

The values represented through β and γ diversity are not easily captured within the α diversity focused BES framework. Local α diversity is required to understand the goods local interacting populations produce, but β diversity represents more abstract values. β diverse ecosystems have value over copies of common ecosystem types, their uniqueness connects them to the overall range of forms found in life on earth (γ diversity). Local ecosystem productivity is irrelevant to the value created by these forms of diversity and vice versa. Local tallies of biological entities cannot represent the full range of biological values as they ignore how the preservation of a range of unique variety is valuable.

Ecosystem services are not the only or original justification for preserving biodiversity. Biodiversity was designed to represent the range of biological features that exist (Soulé 1985; Wilson 1992) including key values overlooked in the search for productivity: heritage and option value. These values are not derived from immediate use and may be difficult to represent economically (Silvertown 2015).

Option Value: Biodiversity is the most direct way to preserve option value. The preservation of a range of biological features is a prudent bet-hedging strategy to account for future uncertainty (Faith 1992; Maclaurin and Sterelny 2008; Lean 2017; Owen et al. 2019; c.f. Maier 2012; Newman et al. 2017). The utility of diverse features of life cannot be accurately known. These values need not only be in their use for commerce or medicine (future monetization). Human preferences may change in their representation of what they find aesthetically appealing or culturally significant. Given that the losses of biological features are irreversible, we need to guard against the risk involved in losing these goods (Arrow & Fisher 1974).

Heritage Value: Heritage value is commonly derived from an entity having cultural significance to a group of people, usually developed over extended periods (Thompson 2000). Just as old buildings or artworks have both an intellectual value, in that they are a record of history and culture, and are of aesthetic value, often because they are a physical representation of the past, so too does biodiversity (Russow 1981; Sober 1986). This creates a relationship between local people and the history of environmental systems. Non-indigenous species can have heritage value too, but indigenous species, due to their historical connection to their native range, tend to have high heritage value. While cultural significance is mentioned in the wider ecosystem service framework, a focus on productivity ignores these values.

These values are more difficult to quantify within the ecosystem services framework but they are still instrumental-anthropocentric values. A sophisticated ecosystem services framework could incorporate them, but when such a framework is skewed towards ecosystem productivity and local species counts, they are undervalued.

4.3. Valuing Diversity

Invasive species should be controlled because they diminish β diversity homogenizing the biological world (Wright 2011). Uniqueness and diversity foster connections between local citizens and their natural landscape, which can be lost through it being just like any other place in the world. This grounds people's local pride in these systems and justifies their disdain for homogenisation. Heritage value is created by local people interacting with their local ecological systems over time. Value is created by the acknowledgement of unique experiences formed by having a relationship to a unique environment. This can be described as a relational intrinsic value or as an instrumental value (Elliot 1992). Heritage and uniqueness increase ecosystem desirability to not just local people but also tourists. There is no reason for me to travel to California to walk through Gum forests. The Gum forests around Sydney provide the same aesthetic experience but also possess heritage value derived from their historical relationship to this place and the other species within the Australian landscape. This provides the Sydney Gum forest with a comparative advantage in its conservation value over the California Gum forest. The cultural services provided by ecosystems are often recognised by ecosystem services in studies (Boerema et al. 2017) but are not represented by the BES relationship built from local species counts.

Global species richness, γ diversity, is of unique heritage value (Wilson 1992). Not only does it provide local people with a unique sense of place in the world, but unique biotic forms carry information about the past. Global species diversity is seen as an object of global heritage, comparable to the collection of human sites like the pyramids of Giza or Stonehenge. Some are sceptical of invoking global heritage, as its protection can take the form of colonialism and as such cannot be ethically enforced (Sarkar 2019). While we can accept that acting on global heritage claims at times can be unethical, we may still hold that such entities are of global value, and as local conservation actors, we should maintain this value. Preserving global species richness is the archetypal commitment of environmentalism. The founding of the International Union for Conservation of Nature and its Red List was created with the goal of stopping global extinctions (IUCN 2020) and The United Nations Educational, Scientific, and Cultural Organization’s (UNESCO) World Heritage List was created to preserve sites of heritage value be they natural or man-made (UNESCO 2021). While conservationists may accept that we cannot save all species, due to resource limitations, it does not imply global species preservation is not a goal of conservation. Advocating for allowing ‘relic’ or ‘loser’ species to become extinct stands in contrast to such aims (Pearce 2015; Thomas 2017). To claim that global species loss is secondary to the primary conservation goal of resource production is to reject the foundations of conservation biology.

The emphasis on local diversity and acceptance of global extinction, proposed by sceptics, stands as a radical rejection of the principles traditionally associated with conservation. Consider the original postulates of conservation described by Soulé (1985): (1) diversity should be preserved, (2) untimely extinctions should be prevented, (3) ecological complexity should be maintained, (4) evolutionary processes should continue, and (5) biological diversity has intrinsic value. Interpreting these postulates as claims about global or local diversity results in different recommendations. By solely interpreting diversity locally rather than globally, sceptics are proposing we, at the minimum, jettison 1, 2, and 5 as global conservation aims. They must defend such a radical change in conservation values.

Invasive species actively diminish β diversity when they eliminate endemic biotic variation and replace them with biotic forms that are found commonly elsewhere. This not only diminishes heritage value but also option value. Option value directly connects to β diversity, as unique features create new options. Option value does not require large standing populations of high productivity species, just preserving unique lifeforms because we may value them in unique and unpredictable ways in the future.

Preserving diverse biotic features directly entails the preservation of unique options, it is just a question of what the best way is to measure diversity to represent the unknown future uses of life on earth (Lean 2017). Attempts to reduce option value to functional diversity (e.g. Mazel et al. 2018) systematically underestimates the value of biotic diversity because they ignore the way human preferences for the environment change over time, often in unexpected ways. While ‘swamps’ were not valued highly in yesteryear, many today highly value ‘wetlands’. Option value indicates we should preserve the environment for changing recreational and aesthetic valuations in addition to its possible immediate economic uses. There is a range of values that people, when surveyed, hold towards the environment that are not captured by productivity (see the literature on Wildlife Value Orientations e.g. Fulton et al. 1996). These values change between demographics and over time.

Option value is for preserving biodiversity so other humans can value different aspects of the environment in the future.

There are numerous ways to describe the value that biodiversity provides. Local species richness is inadequate. Adding rats, cats, and pigeons to every corner of the globe does not preserve the heritage or options value of an area. Possessing unique biotic resources allows communities to bargain with other communities and fosters their connection to the local environment. These values require representing the range of lifeforms that exist across different ecosystems through γ biodiversity and β diversity. These necessary components of biodiversity preservation are ignored when we solely focus on ecosystem productivity.

Now one could argue that this dispute is about differing values rather than equivocation. It is, in one sense. The critics of invasive species management ascent to a much narrower conception of conservations goals than most conservationists have traditionally considered. Only describing biodiversity as α diversity, rather than admitting the importance of β and γ diversity, and representing services as being derived from high productivity and fecundity. They could argue that local species richness is more significant than both heritage and option value. In partial agreement with these critics, some have argued the ecosystem services paradigm justifies not preserving a large portion of biodiversity (Newman 2020). But invasive species critics, however, do not provide strong arguments for such a narrowing of the scope of conservation goals. Instead, they use general terms (biodiversity, ecosystem services) to appear to be agreeing to the more widely held views about conservation. This appears to be a rhetorical decision to equivocate for the means of engagement with conservations aims. What is required of such critics is a direct argument we should narrow the goals of conservation for there to be an honest debate about values in conservation. This would then facilitate the further assessment of the costs and benefits of preferring such a narrow interpretation over the wider goal’s conservation has traditionally held.

5. Conclusion: Beta Diversity and Invasion

Accepting that biodiversity must represent uniqueness and disparity does not imply we must always control Non-Indigenous Species in wild spaces. There are a significant number of species that are endangered or extinct in their native habitat but wild in an invasive habitat. Thompson (2014) frames his discussion of invasive species control around the case of the Camel. Wild Camel populations no longer exist in their native range, but wild Camel populations move through central Australia. If we remove this population, we reduce the β diversity of this habitat and the number of wild populations on earth. Accepting β diversity as a significant biodiversity measure indicates we should retain Camel populations in Australia. This is, however, not without conditions. If an invasive population threatens multiple endemic native populations, it will warrant the control or even eradication of this population. Population control is critical for populations without consumers. Population control does not imply local extinction and often the best choice is to keep the population numbers low enough so that they do not impact indigenous populations.

The β diversity conservation framework does not necessitate invasive species control in all cases. The number of species that are endangered in their native range and invasive are increasing and include the wattle-necked soft-shell turtle, the Monterey pine, and the Barbary Sheep (Marchetti & Engstrom 2016). There will be instances where non-indigenous species have moved into a system and now provide services necessary for the survival of endemic species. Chew (2009) argues Tamarisk in the USA is a critical habitat for native songbirds. In such cases, consideration should be given to these populations and the role they play in supporting biotic diversity and uniqueness. This does not, however, warrant the rejection of invasive species control and eradication.

Current arguments forwarded by sceptics of invasive species control engage environmentalists on their own principles rather than solely forwarding animal welfare arguments. They contest that on the grounds of preserving biodiversity and promoting ecosystem services the control of invasive species is not justified. Their arguments, however, require an impoverished account of biodiversity, one which equates local species counts with biodiversity. This position ignores the importance of diversity and the disparity of life. It ignores the value of unique biotic options, and the potential utility these options could bring, and it ignores the heritage contained in life on Earth. Such values justify the preservation of endemic and unique species even when they are not major contributors to local productivity.

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References

Arrow, K. J., & Fisher, A. C. (1974). Environmental Preservation, Uncertainty, and Irreversibility. *The Quarterly Journal of Economics*, *88*(2), 312-319.

Boerema, A., Rebelo, A. J., Bodi, M. B., Esler, K. J., & Meire, P. (2017). Are ecosystem services adequately quantified?. *Journal of Applied Ecology*, *54*(2), 358-370.

Boltovskoy, D., Sylvester, F., & Paolucci, E. M. (2018). Invasive species denialism: sorting out facts, beliefs, and definitions. *Ecology and evolution*, b*8*(22), 11190-11198.

Cardinale, B. J., Matulich, K. L., Hooper, D. U., Byrnes, J. E., Duffy, E., Gamfeldt, L., ... & Gonzalez, A. (2011). The functional role of producer diversity in ecosystems. *American journal of botany*, *98*(3), 572-592.

Carpenter, S. R., DeFries, R., Dietz, T., Mooney, H. A., Polasky, S., Reid, W. V., & Scholes, R. J. (2006). Millennium ecosystem assessment: research needs. *Science* 314: 257-258

Chew, M. K. (2009). The monstering of tamarisk: how scientists made a plant into a problem. *Journal of the History of Biology*, 42(2), 231-266.

Chew, M.K. and Hamilton, A.L. (2011) The rise and fall of biotic nativeness: a historical perspective. In Richardson, D.M. (Eds) *Fifty Years of Invasion Ecology. The Legacy of Charles Elton.* Blackwell, Oxford, 35–48.

Clavel, J., Julliard, R., & Devictor, V. (2011). Worldwide decline of specialist species: toward a global functional homogenization?. *Frontiers in Ecology and the Environment*, *9*(4), 222-228.

Courtois, P., Figuieres, C., Mulier, C., & Weill, J. (2018). A cost–benefit approach for prioritizing invasive species. *Ecological Economics*, 146, 607-620.

Costanza, R., Fisher, B., Mulder, K., Liu, S., & Christopher, T. (2007). Biodiversity and ecosystem services: A multi-scale empirical study of the relationship between species richness and net primary production. *Ecological economics*, *61*(2-3), 478-491.

Costanza R. (2015). Ecosystem services in theory and practice. In P Figgs, B Mackey, J Fitzsimons, J Irving, P Clark (Eds) *Valuing nature: Protected areas and ecosystem services.* Australian Committee for IUCN: Sydney, 6–15

Daily, G. C. (1997). *Nature's services*. Island Press: Washington, DC.

Dasgupta, P., Kinzig, A. P., & Perrings, C. (2013). The value of biodiversity. In: S. Levin, G.C. Daily and R.K. Colwell et al., (Eds), *The Encyclopedia of Biodiversity*, Academic Press, San Diego, CA

Davis, M. A., Chew, M. K., Hobbs, R. J., Lugo, A. E., Ewel, J. J., Vermeij, G. J., … Carroll, S. P. (2011). Don't judge species on their origins. *Nature*, *474*(7350), 153.

Dirzo, R., & Raven, P. H. (2003). Global state of biodiversity and loss. *Annual review of Environment and Resources*, *28*.

Dornelas, M., Gotelli, N. J., McGill, B., Shimadzu, H., Moyes, F., Sievers, C., & Magurran, A. E. (2014). Assemblage time series reveal biodiversity change but not systematic loss. *Science*, *344*(6181), 296-299.

Elliot, R. (1992). Intrinsic value, environmental obligation and naturalness. *The Monist*, *75*(2), 138-160.

Faith, D. P. (2010). Biodiversity transcends services. *Science*, *330*(6012), 1744-1745.

Faith, D. P. (1992). Conservation evaluation and phylogenetic diversity. *Biological Conservation*, *61*(1), 1–10.

Faith, D. P. (2016). A General Model for Biodiversity and its Value. In J. Garson, A. Plutynski, & S. Sarkar (Eds.), *The Routledge Handbook of Philosophy of Biodiversity*.

New York: Routledge, 69 – 85.

Faith, D. P. (2018). Avoiding paradigm drifts in IPBES: reconciling "nature's contributions to people," biodiversity, and ecosystem services. *Ecology and Society*, *23*(2).

Fulton, D. C., Manfredo, M. J., & Lipscomb, J. (1996). Wildlife value orientations: A conceptual and measurement approach. *Human dimensions of wildlife*, *1*(2), 24-47.

Frank, D. M. (2019). Disagreement or denialism? "Invasive species denialism" and ethical disagreement in science. *Synthese*, 1-29.

Haines-Young, R., & Potschin, M. (2010). The links between biodiversity, ecosystem services and human well-being. In D. Raffaelli & C. Frid (Eds.) *Ecosystem Ecology: a new synthesis*. Cambridge, 110-139.

Hamilton, G. (2010). *Super Species: The Creatures That Will Dominate the Planet.* Richmond Hill: Firefly.

Hendriks, I. E., & Duarte, C. M. (2008). Allocation of effort and imbalances in biodiversity research. *Journal of Experimental Marine Biology and Ecology*, *360*(1), 15-20.

IUCN (2020). *The IUCN Red List of Threatened Species.* Version 2020-2. URL https://www.iucnredlist.org. Accessed 10.10.2020.

Kirkpatrick, J. B., Brown, M. J., & A. Moscal. (1980). *Threatened plants of the Tasmanian central east coast.* Tasmanian Conservation Trust.

Kopf, R. K., Nimmo, D. G., Humphries, P., Baumgartner, L. J., Bode, M., Bond, N. R., ... & Olden, J. D. (2017). Confronting the risks of large-scale invasive species control. *Nature Ecology & Evolution*, 1(6), 1-4.

Lean, C., & Maclaurin, J. (2016). The Value of Phylogenetic Diversity. In R. Pellens & P. Grandcolas (Eds.), *Biodiversity Conservation and Phylogenetic Systematics* Springer, 19–37.

Lean, C., & Sterelny, K. (2016). Ecological hierarchy and biodiversity. In J. Garson, A. Plutynski, & S. Sarkar (Eds.), *The Routledge handbook of biodiversity*. London: Routledge, 110-124.

Lean, C. H. (2017). Biodiversity Realism: Preserving the tree of life. *Biology & Philosophy, 32*(6), 1083–1103.

Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J. P., Hector, A., ... & Tilman, D. (2001).

Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science*, *294*(5543), 804-808.

Luna, P., Corro, E. J., Antoniazzi, R., & Dáttilo, W. (2020). Measuring and linking the missing part of biodiversity and ecosystem function: The diversity of biotic interactions. *Diversity*, *12*(3), 86.

Mace, G. M., Norris, K., & Fitter, A. H. (2012). Biodiversity and ecosystem services: a multilayered relationship. *Trends in ecology & evolution*, *27*(1), 19-26.

Maclaurin, J., & Sterelny, K. (2008). *What is biodiversity?* Chicago: University of Chicago Press.

Magurran, A. E., & McGill, B. J. (2011). *Biological diversity: frontiers in measurement and assessment*. Oxford: Oxford University Press.

Maier, D. S. (2012). *What's so good about biodiversity? A call for better reasoning about nature's value*. Dordrecht: Springer.

Marchetti, M. P., & Engstrom, T. (2016). The conservation paradox of endangered and invasive species. *Conservation Biology*, *30*(2), 434-437.

Marris, E. (2011). *Rambunctious garden: saving nature in a post-wild world*. Bloomsbury Publishing USA.

Mazel, F., Pennell, M. W., Cadotte, M. W., Diaz, S., Dalla Riva, G. V., Grenyer, R., ... & Pearse, W. D. (2018). Prioritizing phylogenetic diversity captures functional diversity unreliably. *Nature Communications*, *9*(1), 1-9.

Millennium Ecosystem Assessment. Washington, DC, Island Press.

Newman, J. A., Varner, G., & Linquist, S. (2017). *Defending biodiversity: environmental science and ethics*. Cambridge University Press.

Newman, J. A. (2020). Biodiversity, ecosystem functioning, and the environmentalist agenda: a reply to Odenbaugh. *Biology & Philosophy*, *35*(1), 1-8.

Odenbaugh, J. (2020). Biodiversity, ecosystem functioning, and the environmentalist agenda. *Biology & Philosophy*, 35(1), 16.

Owen, N. R., Gumbs, R., Gray, C. L., & Faith, D. P. (2019). Global conservation of phylogenetic diversity captures more than just functional diversity. *Nature communications*, 10(1), 1-3.

Pearce, F. (2015). *The new wild: Why invasive species will be nature's salvation*. Icon Books Ltd.

Perrings, C., Naeem, S., Ahrestani, F., Bunker, D. E., Burkill, P., Canziani, G., ... & Kawabata, Z. (2010). Biodiversity Transcends Services—Response. *Science*, *330*(6012), 1745-1745.

Sagoff, M. (2005). Do non-native species threaten the natural environment? *Journal of Agricultural and Environmental Ethics*, *18*(3), 215–236.

Sagoff, M. (2018). Invasive species denialism: a reply to Ricciardi and Ryan. *Biological Invasions*, *20*(10), 2723-2729.

Reyers, B., Polasky, S., Tallis, H., Mooney, H. A., & Larigauderie, A. (2012). Finding common ground for biodiversity and ecosystem services. *BioScience*, *62*(5), 503-507.

Ricklefs, R. E. (1987). Community diversity: relative roles of local and regional processes. *Science*, *235*(4785), 167-171.

Russell, J. C., & Blackburn, T. M. (2017). The rise of invasive species denialism. *Trends in Ecology & Evolution*, *32*(1), 3-6.

Russow, L. M. (1981). Why do species matter?. *Environmental Ethics*, *3*(2), 101-112.

Sarkar, S. (2006). Ecological diversity and biodiversity as concepts for conservation planning: comments on Ricotta. *Acta Biotheoretica*, *54*(2), 133-140.

Sarkar, S. (2012). *Environmental philosophy: from theory to practice*. Sussex: John Wiley & Sons.

Sarkar, S. (2016). Approaches to Biodiversity. In J. Garson, A. Plutynski, & S. Sarkar (Eds.) *The Routledge Handbook of Philosophy of Biodiversity*. New York: Routledge, 375-399.

Sarkar, S. (2019). What Should "Biodiversity" Be? In E. Casetta, J. Marques da Silva, & D. Vecchia (Eds.) *From Assessing to Conserving Biodiversity: Conceptual and Practical Challenges*. Switzerland: Springer, 401–414.

Sax, D. F., & S. D. Gaines. (2003). Species diversity: From global decreases to local increases. *Trends in Ecology & Evolution* 18:561–566

Schröter, M., Van der Zanden, E. H., van Oudenhoven, A. P., Remme, R. P., Serna-Chavez, H. M., De Groot, R. S., & Opdam, P. (2014). Ecosystem services as a contested concept: a synthesis of critique and counter-arguments. *Conservation Letters*, *7*(6), 514-523.

Silvertown, J. (2015). Have ecosystem services been oversold?. *Trends in ecology &*

evolution, *30*(11), 641-648.

Simberloff, D. (2013). *Invasive species: what everyone needs to know*. Oxford University Press.

Sober, E. (1986). 'Philosophical problems for environmentalism'. In B. Norton (Eds.) *The Preservation of Species*. Princeton: Princeton University Press, 173-94.

Socolar, J. B., Gilroy, J. J., Kunin, W. E., & Edwards, D. P. (2016). How should beta-diversity inform biodiversity conservation?. *Trends in ecology & evolution*, *31*(1), 67-80.

Soulé, M. E. (1985). What Is Conservation Biology? *BioScience*, *35*(11), 727–734.

Soulé, M. E. (1996). "Are ecosystem processes enough?" *Wild Earth* 6(1): 59–60.

Srivastava, D. S., & Vellend, M. (2005). Biodiversity-ecosystem function research: is it relevant to conservation?. *Annu. Rev. Ecol. Evol. Syst.*, *36*, 267-294.

Thomas, C. D. (2013). The Anthropocene could raise biological diversity. *Nature*, *502*(7469), 7-7.

Thomas, C. D. (2017). *Inheritors of the Earth: how nature is thriving in an age of extinction*. Hachette UK.

Thompson, J. (2000). Environment as Heritage. *Environmental Ethics*, *22*(3), 241-258.

Thompson, K. (2014) *Where do camels belong? the story and science of invasive species.* Profile Books, London.

UNESCO (2021). *World Heritage Convention.* URL https://whc.unesco.org/en/convention/. Accessed 03.08.2021.

Vane-Wright, R. I., Humphries, C. J., & Williams, P. H. (1991). What to protect?—Systematics and the agony of choice. *Biological Conservation*, *55*(3), 235–254

Vellend, M. (2017). The biodiversity conservation paradox. *American Scientist*, *105*(2), 94-101.

Wallach, A. D., Bekoff, M., Batavia, C., Nelson, M. P., & Ramp, D. (2018). Summoning compassion to address the challenges of conservation. *Conservation Biology*, *32*(6), 1255-1265.

Wilson, E. O. (1992). *The diversity of life*, Cambridge: Belknap Press.

Whittaker, R. J., Willis, K. J. & Field. R. (2001). "Scale and species richness: towards a general, hierarchical theory of species diversity." *Journal of biogeography* 28.4: 453-470.

Winfree, R., W. Fox, J., Williams, N. M., Reilly, J. R., & Cariveau, D. P. (2015). Abundance of common species, not species richness, drives delivery of a real-world ecosystem service. *Ecology letters*, 18(7), 626-635.

Wright, S. (2011). Invasive species and the loss of beta diversity. *Ethics & the Environment*, *16*(1), 75-97.

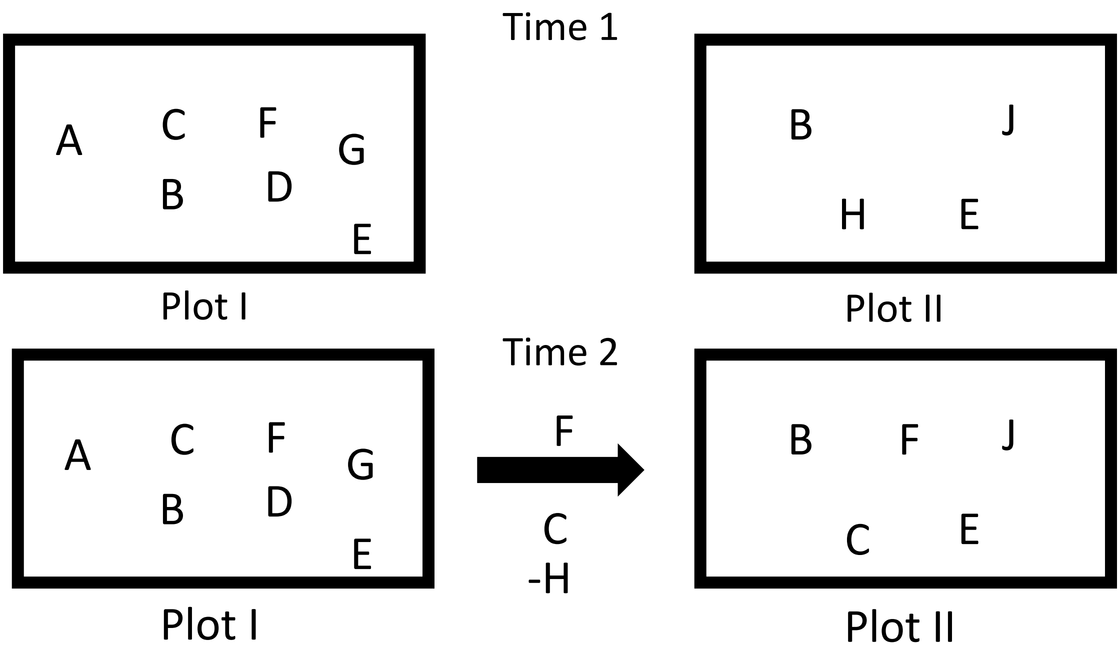

Figure 1. Plots, I, which contains 7 species, and II, which has 4 (α diversity). II adds two unique species to I (β diversity). Their combined species count is 9 (γ diversity). If through introduction, two of I's species (F,C) invade II, and one of II's unique species (H) is eradicated then II increases its α diversity by 1 but its β diversity is reduced by 1.